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The evolution of the Hepaticæ.

Vice-presidential address before section G, A. A. A. S.

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There is, perhaps, a natural tendency among specialists to magnify the importance of the particular subject or group of life forms in which they happen to be specially interested. The horticultural botanist, dreaming of the time when the world will be reorganized through the products of his art, is prone to see nothing beyond utility and ornament in plants, and it becomes a part of his nature to see some useful character in forms of vegetation which to others are devoid of either beauty or utility. The economic mycologist, over-impressed with the magnitude of the losses sustained by the unfortunate agriculturist and fruit grower, is haunted in sleep with visions of anthracnose and mildew, and in his waking hours sees little in botany but host-plants bristling with parasites and Bordeaux mixtures certain to relieve them of their incubus. The man with inherent, if not coherent, proclivities for priority, with a war-like temperament and a strong tendency to cross lances, sees in botany one vast battle field of synonymy in which cohorts of pre-Linnaean binomials, hordes of decapitalization dogmas, hostile homonyms and Kuntzian curiosities charge down upon each other in battalions, form and *reform* in utter confusion. There are some microscopic botanists whose degree of specialization never permits them to look outside the limits of an apical cell; and others still whose botanical horizon is bounded by the field of an immersion lens and whose azimuth and right ascension are calculated within its limits. We are all more or less inclined to ride our own hobbies in public places, so in performing the initial function of this office, I can perhaps do no better than to bring forth mine. In this way, I shall at least be in touch with present custom.

With no desire, however, to overestimate its importance, I wish to place before you the position in the botanical system of a comparatively obscure group of plants and to call your attention for a brief time no less to their own differentiation than to their important relation to the evolution of the plant world. I desire to set forth in something of a reasonable way the characters of the group and to correct some misunderstandings that have resulted from an imperfect appreciation of its relations. The group commonly known as Hepaticæ has suffered at the hands of general botanists, and through them an incomplete and one-sided conception is transmitted to the generation of botanical students now coming to their maturity. The average text-book of botany emphasizes strongly the representative character of Marchantia polymorpha. In elementary laboratory guides, this is even made to stand as the sole representative of all the bryophytes. In those somewhat more comprehensive, it is made a type of the more limited group, the Hepaticæ, and in even the most complete it is made to stand pre-eminent as the representative of this triply developed group of plants, notwithstanding the fact that the other members of this trio are vastly more important—one in the nature and extent of its development *per se*, and the other in its important relations to the development of the higher groups of the plant world. One elementary text-book that has in general done much to elevate the standard of botanical teaching in America during the past decade opens its account of the Hepaticæ with these words: "In the liverworts the plant body is for the most part either a true thallus or a thalloid structure. When there is a differentiation into stem and leaves," etc. This statement may be taken as fairly representing a conception of the group common among botanists and botanical teachers. The hepatics among us are popularly supposed to be thallose or thalloid plants and Marchantia is regarded as a normal representative. As opposed to this wide-spread misconception, it should be noted that as far back as the date of the last publication of a general synopsis of the Hepaticæ (1847) the relative numerical importance of the Marchantiaceæ was only 17 per cent. of the entire group and the increase since that time has been even more largely in the direction of the other groups, especially the foliaceous Jungermaniaceæ which represent at once the most numerous and best differentiated

types of the Hepaticæ.[1] It would be even less a misrepresentation of the Musci to make its representatives in Andreaea, Phascum or Buxbaumia than to place Marchantia or any of its allies as a normal representative of the Hepaticæ. Armed, however, with such a conception gained from the elementary texts and emphasized by the works of reference usually accessible in an ordinary laboratory, as for example Kny, Strasburger, Sachs, and Goebel, the student goes forth into the field to study liverworts and after he has exhausted Marchantia and Conocephalus, and has possibly seen a Riccia, he is usually stranded and knows not what to seek. In fact, many are more likely to confuse some such thallose lichen, as Peltigera, with liverworts than to look for them among leafy forms which their training has not rendered them able to properly correlate. The Lophocoleas, the Cephalozias, the Frullanias and the Radulas, so elegant in their structure as to impress the least æsthetic student with their beauty, so diversified in their evolution as to demand the exercise of his most active powers of reflection, and withal so simple in structure as to render them accessible with a minimum of microscopic technique—these are a closed volume to him because of the limitations of his early instruction and impressions.

The group known since the time of Adanson as the Hepaticæ stands in a unique position on the boundary line of thallose and leafy plants, and its position is not only intermediate from the structural standpoint, but in its relation to the evolution of the higher plants it stands as a key or link between the lower and simpler and the higher and more complex. The group is not a compact one nor are its component groups closely united to each other. It is even to be doubted if a good reason exists for the separation of the bryophytes into the two classes Musci and Hepaticæ, and it would be hazardous to attempt their separation as coordinate groups on any rational grounds, even if we leave in question their relation to the Sphagnaceæ.

[1]The relative extent of the Jungermaniaceæ as developed by modern exploration and subsequent study can be seen in a comparison of a few representative genera:

	Species described in Synopsis Hepaticarum 1844–47.	Species reported by Schiffner 1893.
Metzgeria	8	36
Lophocolea	69	149
Plagiochila	179	463

The hepatics possess almost absolutely no utilitarian aspect. Beyond the doubtful use of one or two in medicine, and the occasional occurrence of one or more tropical species as weeds, they are, so far as the physical condition of the human race is concerned, an entirely useless group of plants. They do not trouble the experiment station botanist, the horticulturist finds no use for them, and the general public does not see sufficient importance in them to subscribe a single shilling for the endowment of a laboratory for research in such an apparently barren field. And yet from the higher standpoint of genetic relationship, there is probably no single group of plants that occupies such an unique position in the plant world. What the comprehensive and heterogeneous group "Vermes" is to the animal kingdom, the Hepaticæ are to plants, with this difference, that we have here a much less complicated group of organisms with which to deal.

To understand more fully the relation of the Hepaticæ to the evolution of the green plants and particularly to their role in the development of the alternation of phases of reproduction which has attained such extended proportions in the ferns and other pteridophytes, it is desirable to bring in brief review the successive stages in the processes of reproduction from the simplest forms upward. For it must be remembered that even if the methods of reproduction cannot serve as the means of separating the primary types of the thallophytes in a natural system of classification, they nevertheless represent the highest function that is manifested in organic life. The successive stages may be characterized as follows:

I. Among forms whose only method of reproduction consists of fission, in which the individual life begins with the completion of the karyokinetic process of cell division and closes when its individuality is lost in the next generation produced, the type of the life history of the organism may be represented by a straight line whose terminations bear no relation to each other. There is no round of life history, no cycle of development where fission is the law of reproduction.

II. Among forms in which conjugation occurs, we have successive stages of distinct sexual reproduction occurring before the idea of bisexuality has been differentiated. Two purposes seem involved in this process, (1) the increase of vitality by the union of elements of separate origin, and (2) the production of a structure capable of holding vitality more

certainly through critical changes of environment; hence the resting-spore. We have here a type of life history where continuity commences to curve into a circle and its ends begin to unite to form a complete cycle of development. In many forms, however, the individual is too hopelessly entangled in colony life to be clearly separated.

III. In forms (like Vaucheria) where the sexual cells are clearly distinguishable from the early commencement of the process of reproduction, and the oospore results directly and simply from the act of fertilization, the life history of the plant may be clearly said to be represented by the circle. The phase of growth is purely a sexual one from spore to germinating filament through the production of sexual apparatus to spore again. If asexual reproduction occurs, it merely serves to rapidly multiply the plant when favoring environment makes it possible, and bears no relation to the sexual process and is not dependent upon it.

IV. Among some of the higher algæ occurs the simplest form of alternation of phases of reproduction. While there are various modifications of the process in minor details in many groups of algæ, the act of fertilization in certain representative forms is followed (1) by the formation of a special envelop of cells about the oogone as a specialized protective covering, and (2) by the division of the cell contents of the oogone into a series of reproductive bodies, an asexual process following as a result of a sexual one and therefore dependent on it. The life history here, instead of representing a simple cycle of growth, can be best characterized as a combination of two loops each short of a circle, the larger representing the sexual stage from germinating spore to the completion of the process of fertilization, and the smaller representing the asexual phase involved in the internal cell division that results in the development of the reproductive bodies. The so-called "alternation of generations", which is nothing more than the succession of phases in the life history of the organism, commences at a point considerably below the lowest bryophytes.

V. The transition from the above condition to that which we find in the lowest archegoniates is a simple one. The advance manifests itself in the following particulars: (1) in the protective envelop of the egg cell being developed prior to the act of fertilization and not as a result of it; (2) in the some-

what more complex development of the asexual phase (sporogone) in the formation of a definite multicellular wall and the division of the interior by a double process of cell multiplication. Most of these details even are more or less feebly foreshadowed in some of the higher algæ. The only modification necessary in the diagrammatic representation of the lower bryophytes as contrasted with that of the higher algæ is the relatively greater development of the asexual phase which is therefore represented by a proportionally larger loop. The lines of specialization which have resulted from the varied differentiations of this simple type will be discussed more in detail later in this paper.

VI. The highest development of the principle of alternation of phases of reproduction is illustrated by the well known climax reached among the pteridophytes in which the asexual phase represents a degree of specialization utterly disproportionate to the simple sexual phase (prothallus) which has scarcely advanced beyond the primitive condition reached by the lowest archegoniates. The diagrammatic representation of the life history of the fern is therefore a reversal of that of the higher algæ, the larger loop representing the highly differentiated asexual phase and the smaller the simple thallose sexual phase.

The high degree of differentiation of the asexual phase of the pteridophytes coupled with the great antiquity of the group have rendered them a stumbling block to many who have not been careful in tracing their homologies. In the evolution of the pteridophytes, however it must be remembered that the line of descent must be sought, not in a comparison of the highly developed asexual phase of the one with the simple sporogone of the other but along the line of the simpler sexual phase. When we consider this feature of the development in its proper light, the progress of evolution from alga to fern is greatly simplified and the distance between the groups either in the time necessary for the derivation of the one from the other or in the slight degree of differentiation manifest in these coordinate phases, is reduced to a minimum. From higher algæ to simple prothallus the transition is not a difficult one. In regard to the other feature of the problem, it may be suggested that the development of the asexual phase of fern-like plants which dates back to the Devonian and reached a high degree of specialization in the Carboniferous,

may have been strongly influenced and perhaps rapidly evolved by the peculiar environment of precarboniferous times; at least the statements of the books in reference to the excessive amount of carbonic oxide in the atmosphere being peculiarly adapted to the growth and development of the lower pteridophytes would support such a hypothesis. On this point, however, it may be questioned whether the statements of the books do not need some modification.

I have said that the Hepaticæ have undergone a triple differentiation. Commencing with a simple thallose plant with its unmodified sporogone, it is evident that there are three possible lines of specialization: (1) the development of the thallus as such; (2) the transformation of the thallus into a leafy axis combined with the modification from creeping to ascending or erect habit; and (3) the specialization of the sporogone at the expense of the thallus. Even a cursory acquaintance with the diverse structures that are developed in the group will make it evident that the Hepaticæ have improved their opportunity in each of these three possible lines and have carried the differentiation of each line to a high degree of perfection. Let us follow out in some detail these three lines of development.

I. *The Marchantiales.* We must place as lowest in the series the group which commences with such simple types as Riccia and Tesselina and ends with the elaborate Marchantia and its congeners. Among the lowest types the habit is not greatly different from that of the algæ, the plants either floating in water or attaching themselves to wet soil. The capsular development in the lower forms moreover is not very diverse from that of certain of the higher algæ, the sporogone being without stem and often imperfectly surrounded by a capsular wall. As we advance to higher forms, we find not only an extensive modification of the thalloid structure necessitating an elaborate system of stomata and in many cases specially modified branches for the better accommodation of the reproductive bodies, but also a striking advance in the capsular development in which the egg cell develops not only a capsule or fertile portion, but also a stalk or sterile portion, which with the addition of elaters formed within the capsule, better serves to distribute the spores.

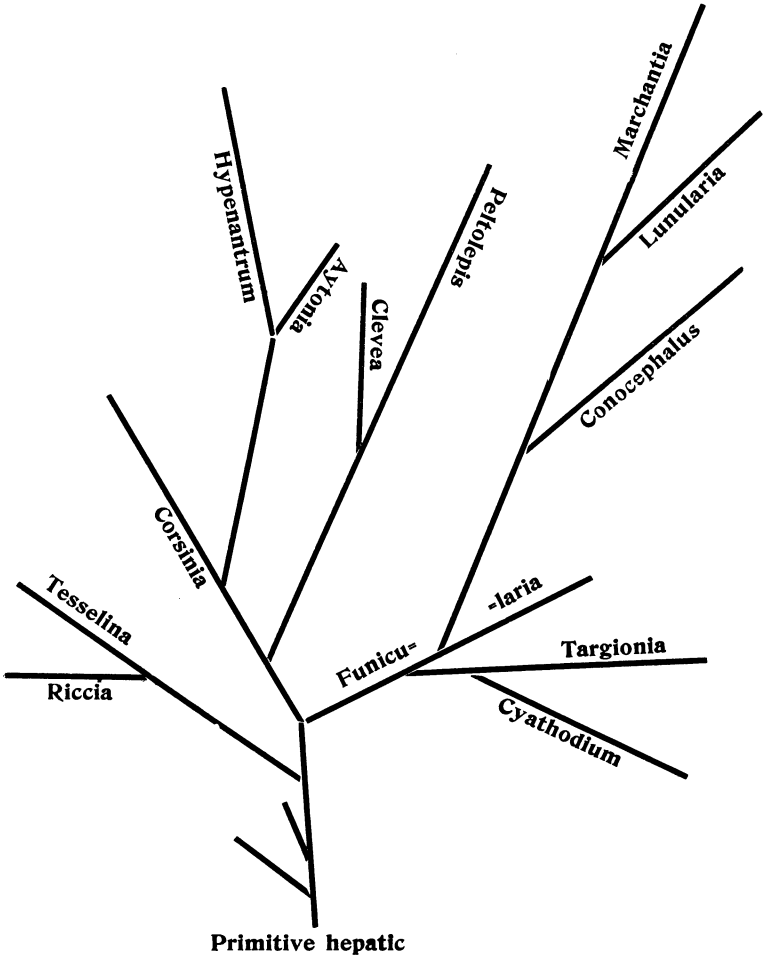
We may note here also two types of differentiation in the specialized branch that bears the carpocephalum, as it ex-

plains some seeming anomalies in the fruiting habits of some of our common Marchantiaceæ. The impression has prevailed and is now wide spread that while Marchantia may commonly be found in fruit, Conocephalus rarely produces it. The fruiting branch of Marchantia is developed before the maturity of the sporogone is reached. This branch is therefore firm and consequently persistent. The botanist who only rarely comes in contact with plants except as they are preserved in herbaria or imbedded in celloidin has considerable opportunity to see the fruit bearing branches of Marchantia as they are developed, long before the spores are mature and persist long after the spores are scattered. On the other hand, Conocephalus, whose archegones are fertilized during the late summer or early autumn, matures its capsules within the carpocephalum before the fruit bearing branch of the thallus is developed. In this condition it passes the winter and with the earliest return of spring the reserve material of the thallus rapidly aids in sending up a semi-hyaline slender branch which lasts barely long enough to allow the capsules to burst through their calyptræ and then withers away. By the time the spring botanist, roused from his hibernation, goes forth to search for Anemone or Epigæa, Conocephalus has long since scattered its spores, its fruiting branch is withered, and the late observer concludes that it rarely produces fruit. He who will become a botanist in any broad sense must come in contact with nature face to face at all seasons, and study plants as they grow, as well as in the herbarium and laboratory. The man who sees and studies plants *only* as they are represented by dried herbarium fragments or in accordance with the stereotyped formula, "treated with a one per cent. solution of chromic acid, stained in mass with picrocarmine, imbedded in paraffine and cut with a Minot microtome," is sure to get a one-sided notion of the true homologies of the vegetable world.

While all the minutiæ of the relations of the Marchantiales have not been worked out, the following provisional arrangement (see diagram opposite) will give some idea of their affinities.

From simple forms like Riccia, themselves doubtless a considerable advance over the primitive hepatic, we find slight modification in Ricciocarpus and Tesselina, and slightly more differentiated forms in Corsinia and Funicularia. To the former are allied such higher forms as Clevea, Aytonia and

Hypenantrum; from forms allied to the latter we have on the one hand Cyathodium and Targionia with their sessile fruit, and on the other, Lunularia, Conocephalus and Marchantia,



which justly may be regarded as the highest thalloid development that appears among the Hepaticæ.

II. *The Jungermaniales.* The second line of differentiation among the Hepaticæ is in the direction of the formation of a leafy axis. From such thalloid forms as Aneura with a

scarcely developed central axis to such simple modifications as appear in Pallavicinia and Metzgeria, in which the central axis becomes distinctly differentiated from the plain wing-like border a single cell in thickness, it is an easy step to pass to such pseudofoliaceous forms as Schiffneria, Fossombronia and Haplomitrium. From these forms again it is not difficult to pass to some of the simpler leafy axes like Lophocolea, Bazzania, and Jungermania. It is in this group that we find the Hepaticæ attaining their greatest profusion of structure, the most remarkable diversity of foliar development, the widest range of adaptation, and the consequent abundance of genera and species that span the world from the lone and barren island of Kerguelen in the south to the inhospitable region of Spitzbergen in the north. Here some three thousand species have been developed, and judging from the rapidity of the returns, it is evident that the tale is not nearly told.

It is, of course, impossible, within the limits of the time assigned, to attempt to touch upon the numerous features of the evolution which this group has undergone in diverse quarters of the world; we can only hint at some of the more striking by way of illustration.

1. The protonemal development among the Jungermaniales is usually slight and ephemeral; in only occasional instances do we find it persistent. Perhaps the most striking illustration of this is Protocephalozia, in which the formation of leaves occurs only as a special development for the protection of the reproductive bodies. The antherids are borne singly in the axils of rudimentary leaves while the perianth, subtended by slender involucral leaves, rises directly from the original protonema which represents the entire vegetative condition of the plant.

2. The lines of development leading from thallose to leafy forms are numerous among the Jungermaniales, and all of them have not yet been definitely correlated. Certain it is that there is no single line of thallose genera as distinct from the foliaceous ones. While the greater part of the thallose forms do not produce their fruit terminally and hence may be separated into a distinct family which may be called the *Metzgeriaceæ* from its typical genus, there are several instances in which thallose forms lead up toward foliaceous forms with which they agree in the closer relation of sporogonial development, as well as in the more important fact that they bear

the sporogone terminal on the main stem or on a branch. The line of this character that is best known is perhaps that leading up to the Trigonantheæ from Zoopsis to Cephalozia. From the simplest thallose structure, differing only slightly from algæ, the various species of Zoopsis become developed so as to present the successive modifications of a leaf of a single cell, a leaf of two cells, and a leaf of four cells; from these steps the passage is easy to such simple two-toothed decurrent leaves as we see developed in some of the Cephalozias, especially in our common Cephalozia multiflora. The fruiting characters in this series are so strikingly alike that they have even been united in a single genus.

3. Perhaps no single group presents so many modifications in the diversity of foliar structure as is manifested in the various genera of the Jungermaniales. With nothing but leaf cells forming a more or less well developed lamina, the greatest conceivable variety of form coupled with modification arising from environment has been differentiated, and we find numerous examples of marvellous adaptation of means to end. From these we may note the simple tripartite leaves of Blepharostoma made up of simple rows of cells; the intricately divided leaves of Trichocolea and Ptilidium which give to the species of those genera their peculiar tomentose appearance; the ciliary fringes of endless variety that characterize the numerous species of Plagiochila; the median lamina of Schistocheila recalling a similiar development in Fissidens among the true mosses, and above all the innumerable paraphyllia of Stephaniella, often covering the entire surface of the leaf. These merely indicate a few of the possibilities of the foliar development. In the leaf cells themselves, we have every grade of compactness, varying from the lax structure of Cephalozia, Chiloscyphus and Kantia to the close compact structure of Herberta and Gymnomitrium.

But beyond all these are the various forms of complication of leaves clearly adapted to serve as retainers of moisture. From the simple folds in the leaves of Radula, Scapania and Diplophyllum, we pass to the basal pockets of Lejeunea which are sometimes elaborately differentiated, and the water sacs of Jubula, Frullania and more especially Polyotus in which they are sometimes developed in great profusion. As might be expected, these peculiar foliar adaptations for holding moisture most prominent in those species that have been driven

from their normal habitat on the ground and on decaying logs to the bark of trees and even the surface of leaves, which in tropical countries are often wholly covered with various species of Lejeunea,[2] together with an occasional Radula and rarely species of other genera. The reputed symbiosis of rotifers and other small animals with these water sacs of Lejeunea and Frullania has been commented on by many observers.

4. No less remarkable is the development of the perianth which serves as a special protection to the maturing sporogone. This is normally free from the uppermost stem leaves, which are usually modified from the ordinary form. In certain genera like Nardia, Marsupella, Schistocheila and Harpanthus, the perianth becomes more or less adherent to the involucral leaves and in some instances forms a bulbous or gibbous enlargement at the base. An exaggeration of this bulbous development produces the marsupiocarpous condition found in Kantia, Geocalyx, Tylimanthus and several other genera, in which the sporogone is developed at the base of a pendulous pouch which penetrates the substratum, or in the tropical Tylimanthus is hung among the stems of various mosses which grow in its vicinity. It is of interest to note that this condition has been developed independently in widely different sections of the family and cannot be considered as forming a tribal alliance by itself as was formerly maintained.

It must now be evident that the Jungermaniales, above all other Hepaticæ, are the types in which the most elaborate development has taken place and that they must furnish the typical representatives of this class. When we add to the great degree of differentiation, the wide-spread geographic distribution of the Jungermaniales which has resulted in populating almost every available island in the world, frequently with endemic species, it becomes evident that we must attribute a great antiquity to the group. The comparative absence of the hepatics in fossiliferous rocks, for obvious reasons, should count as little in determining their antiquity.

III. *The Anthocerotales.* Having considered the two groups in which the hepatics have disported themselves as such, we

[2] I have only once found our Lejeunea calcarea in Indiana. In that instance, it completely covered a small leaf of Camptosorus growing in the damp moss of a ravine. This is the first instance known to me of Lejeunea growing as an epiphyte in northern latitudes.

come finally to the group in which their development has looked toward something higher in the plant world. If the Marchantiales have elaborated the thallus at the expense of other parts, and the Jungermaniales have developed leafy axes and exhausted their energies in the elaboration of beauty and intricacy of foliar development, the Anthocerotales have found a more important line in which to differentiate, namely, the development of the sporogone. And while it has resulted in small returns when considered from a hepatic standpoint, the results otherwise are commensurate with the whole range of higher plants from mosses to Compositæ.

In the Anthocerotales, the thallus has undergone only a slight differentiation from the primitive type; the sporogone, however, develops into a fleshy structure that frequently requires stomata for its transpiration processes. The capsule is necessarily a somewhat permanent structure and unlike all other bryophytes, develops its spores continuously from above downward.

The ancestors of Anthoceros and Notothylas on the one hand, and the Musci on the other, were doubtless the same, and the line of separation between them probably commenced at an early day, since the elaboration of genera and species is no less marked in the Musci than in the foliaceous Hepaticæ.

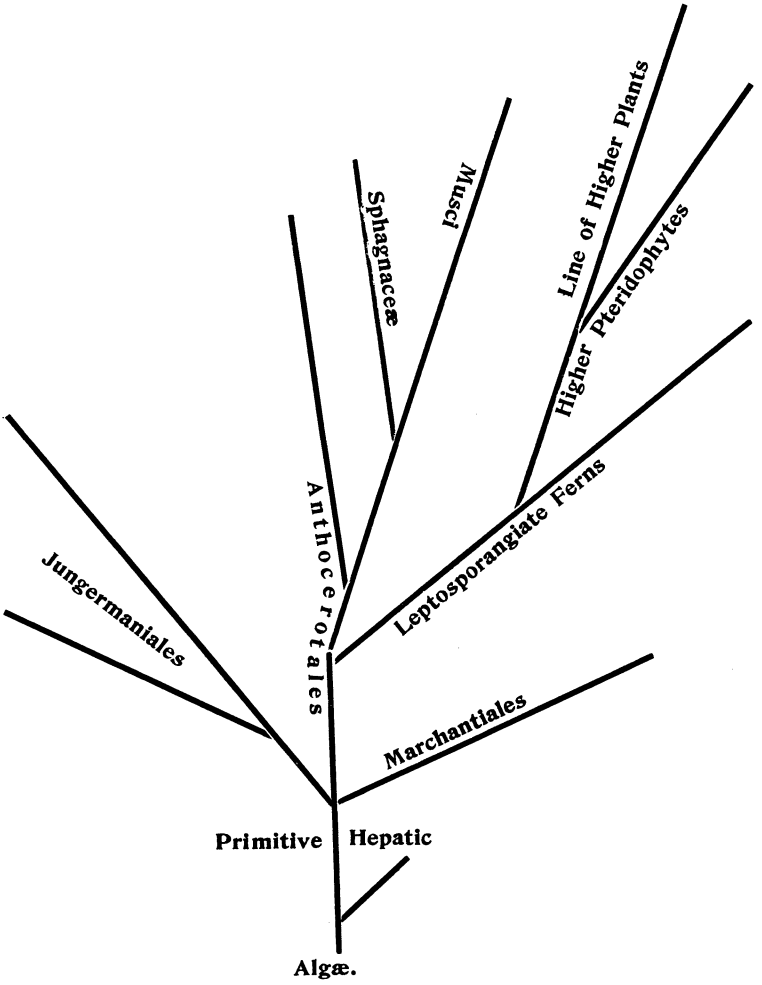
It has further become evident that the line of development of the leptosporangiate ferns, leading upward to the line of the higher plants, is to be sought as a branch from the primitive Anthocerotales. While more investigation is necessary in this direction, the general relations may be indicated by the diagram on the following page.

The early forms of Anthoceros were not swerved from their purpose; they have continued the development of the sporogone at the expense of the thallus and today stand unique among the Hepaticæ. They differ as widely from all other members of the group as do the Musci and Sphagnaceæ and, for this reason combined with others, the class Hepaticæ has little reason for further existence in our system of classification. A reorganization becomes necessary as soon as the remaining bryophytes can be properly co-ordinated.

We can then summarize the relations of the Hepaticæ.

1. The group is not of recent origin. This is shown not only from the wide-spread geographic distribution of its ma-

jor group, and its extensive modification into diverse genera, but as well by its relations through the Anthocerotales to higher groups which have themselves a high antiquity.



2. The group is not a compact one, nor is it entirely circumscribed. The three groups of the Hepaticæ above outlined differ as much or more among themselves as the remaining bryophytes differ from them. There is a necessity for a new grouping of the bryophytes to accord with our present

knowledge. The present grouping into Musci and Hepaticæ as coordinate classes, is entirely unsatisfactory, and artificial.

3. In such a triple development as exists among the Hepaticæ, no single plant can stand as a type which will fairly represent the entire group. If a single plant is to be considered, however, it would be only fair to make the selection from the group which is at once the most highly specialized structurally and the most widely represented in all parts of the world. To the Jungermaniales, and not to the Marchantiales, belongs this distinction.

4. We must recognize at least five families among the Hepaticæ. Among the Jungermaniaceæ, it is well to separate those forms in which the archegone terminates the growth of the shoot from those in which the archegone is distinctively a lateral development. The "Jungermaniaceæ anakrogynæ" of Leitgeb and Schiffner, which will include many but not all of the "Jungermaniaceæ thallosæ" of previous writers, may well be separated as a distinct family for which we propose the name METZGERIACEÆ. The older name, Jungermaniaceæ, may properly be retained for the remaining part of the family which includes by far the greater number of genera and species.

5. The Hepaticæ are especially interesting as constituting the connecting link in the evolution from thallophytes (algæ) to the higher plants. In this particular, the line of the Anthocerotales in which mere vegetative function is sacrificed for the sake of reproductive function, represents the royal line of development.

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